

# Origins and Relationships among the Animal Phyla

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Conceptual and factual advances in the study of animal phylogeny have emerged from recent work in palaeontology, functional morphology and comparative embryology. Many earlier proposals on the origin and relationships of the animal phyla can now be seen to be erroneous.

The fossil record of the Precambrian and early Cambrian has not revealed links between phyla, but it places the time of origin and radiation of the metazoan phyla at earlier than 700 million years ago. Functional morphological studies have raised many possibilities of the convergent or parallel evolution of phyla, especially among those of simpler body construction. In particular, these studies have called into question the validity of hypothetical ancestors and of a monophyletic origin of the Metazoa.

Comparative embryology remains a major source of positive information about the relationships between the animal phyla. Two major assemblages, the spiral cleavage assemblage and the deuterostome assemblage, can be identified by this approach. More information is needed on a number of phyla.

A synthesis of all three lines of investigation emphasizes the likelihood that metazoans arose from protozoans on several occasions.

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## INTRODUCTION

A student once wrote in an essay for me, 'Phylogenetic relationships is a very doubtful area of zoology'. This a sentence of delightful ambiguity. I think all zoologists would agree with it, but for different reasons. To some, the word doubtful would mean dubious, questionable, verging on the disreputable. To others, quite a strong group, the doubt would be as to whether phylogenetic relations is a part of scientific zoology at all. A third group, however, would take it that there are still matters of doubt and unresolved questions concerning animal phylogeny, and would regard this as an important challenge for zoologists to struggle with. I subscribe to the last of these views, but I am well aware that there are plenty of dubious phylogenies as well as some spectacularly unscientific ones in the recent literature. I shall mention some of these as we proceed. I am also aware that a lack of suitable factual knowledge leaves many questions still unanswered concerning phylogenetic relationships, but I think we have now reached the stage where some firmly-based statements can be made.

Many attempts have been made over the years to evaluate the origins of the metazoan phyla and their phylogenetic relationships. Until quite recently there was a strong tendency among animal phylogeneticists to vie with one another in the erection of monophyletic trees for the Metazoa, branching in various ways. Figs 1 and 2 show two examples of this.

Preconception was the basic philosophical stance in these attempts, with the known facts being used as hooks from which to suspend the imagined tree. This approach has not lost its vogue. Papers are still being published which contain trees of this type, replete with nonfunctional hypothetical ancestors. A good example of this, first published in 1976, is shown in Fig. 3. Such works are of the same conceptual status as land bridges in biogeography.

In the last twenty years, however, and especially in the last decade, very substantial conceptual and factual advances have been made by many workers

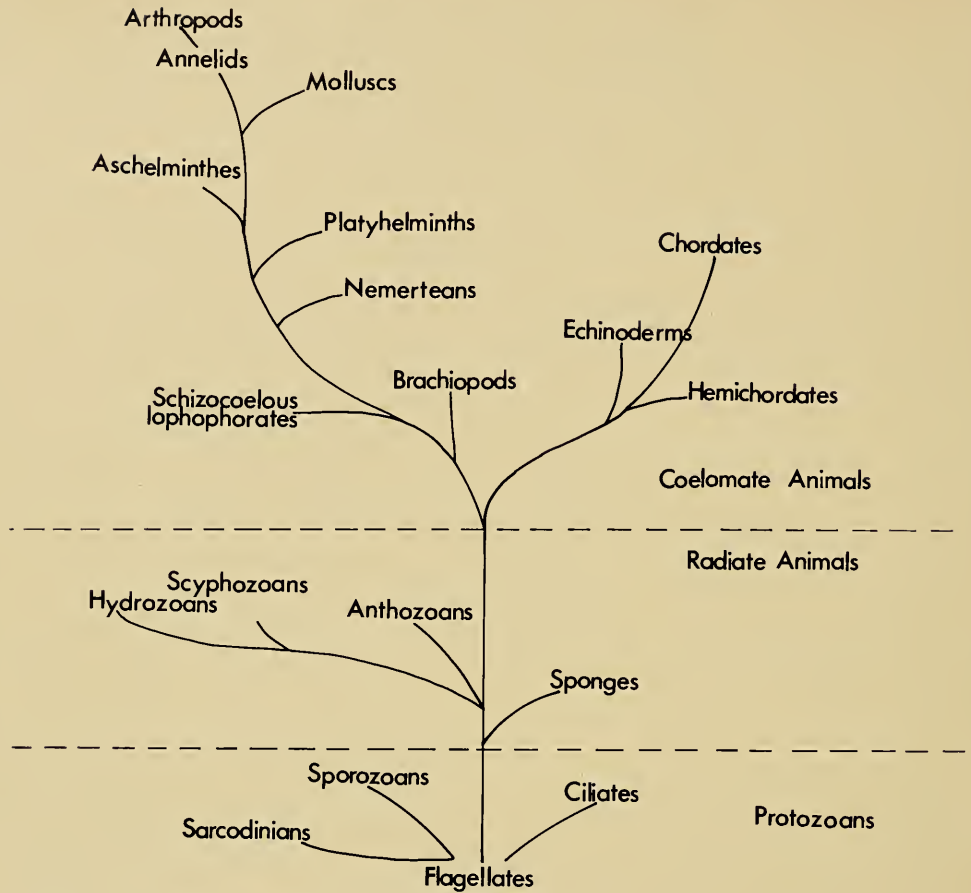


Fig. 1. The phylogenetic tree of Marcus (after Barnes, 1968).

interested in the problem of metazoan phylogenetic relationships. It may seem perhaps surprising that this problem, which was at the forefront of zoological thinking in the latter part of the nineteenth century, should receive a revival of interest in the latter part of the twentieth century; but I think this can be explained by the importance of phylogeny to zoology as a whole. Zoology, the science of animals, is couched in terms of generalizations based properly and entirely on an acceptance of the view that evolution has occurred. The better we understand this evolution in terms of origins and lineages, the better will be our generalizations about its products.

#### CONCEPTUAL ADVANCES

What then are the conceptual advances which are assisting in this endeavour? There are three. The first is a greater emphasis on the notion that facts take precedence over preconceptions. Paraphrasing two famous pragmatists, Sidnie Manton and Henry Ford, hypothetical animals are bunk! The hypothetical urcrustacean shown in Fig. 4 and the hypothetical ancestral mollusc well known amongst zoologists (Yonge and Thompson, 1976), while of value in comprehending the phyla to which they are ascribed, have no place in thinking about the relationships between phyla. Gaps in the evidence must be accepted for what they are and not filled with inventions to satisfy the urge for a monophyletic oversimplification.

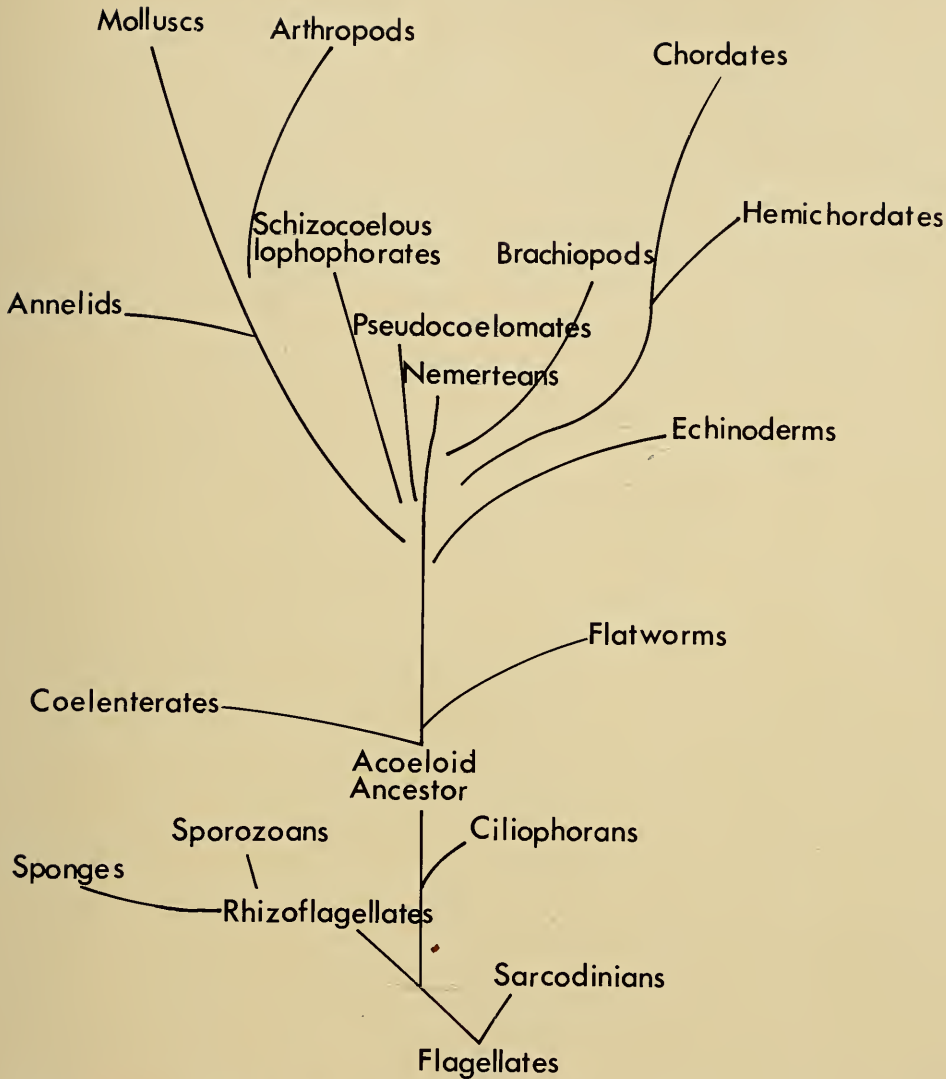


Fig. 2. The phylogenetic tree of Hanson (after Barnes, 1968).

Secondly, deriving from advances in many aspects of zoology, it is now realized that animals exist as functionally integrated complexes of dynamically interacting components, in which there are intrinsic constraints on change as well as the possibilities of change over evolutionary time. Putting this more simply, evolution must be functional and function must be viewed holistically. Any phylogenetic proposal which ignores the requirements of functional gradualism (Anderson, 1967; Dullemeijer, 1980) must be wrong. This is not to say that any proposal based on holistic functional thinking must be right. There are other ways in which error can potentially creep in. Functional thinking may, for example, be employed spuriously to give credence to imaginary evolutionary sequences. Gutmann (1981) treats the deuterostomes in this way, expounding the evolution of all deuterostomes from a segmented chordate stem, itself evolved by an entirely hypothetical 'functional' route.

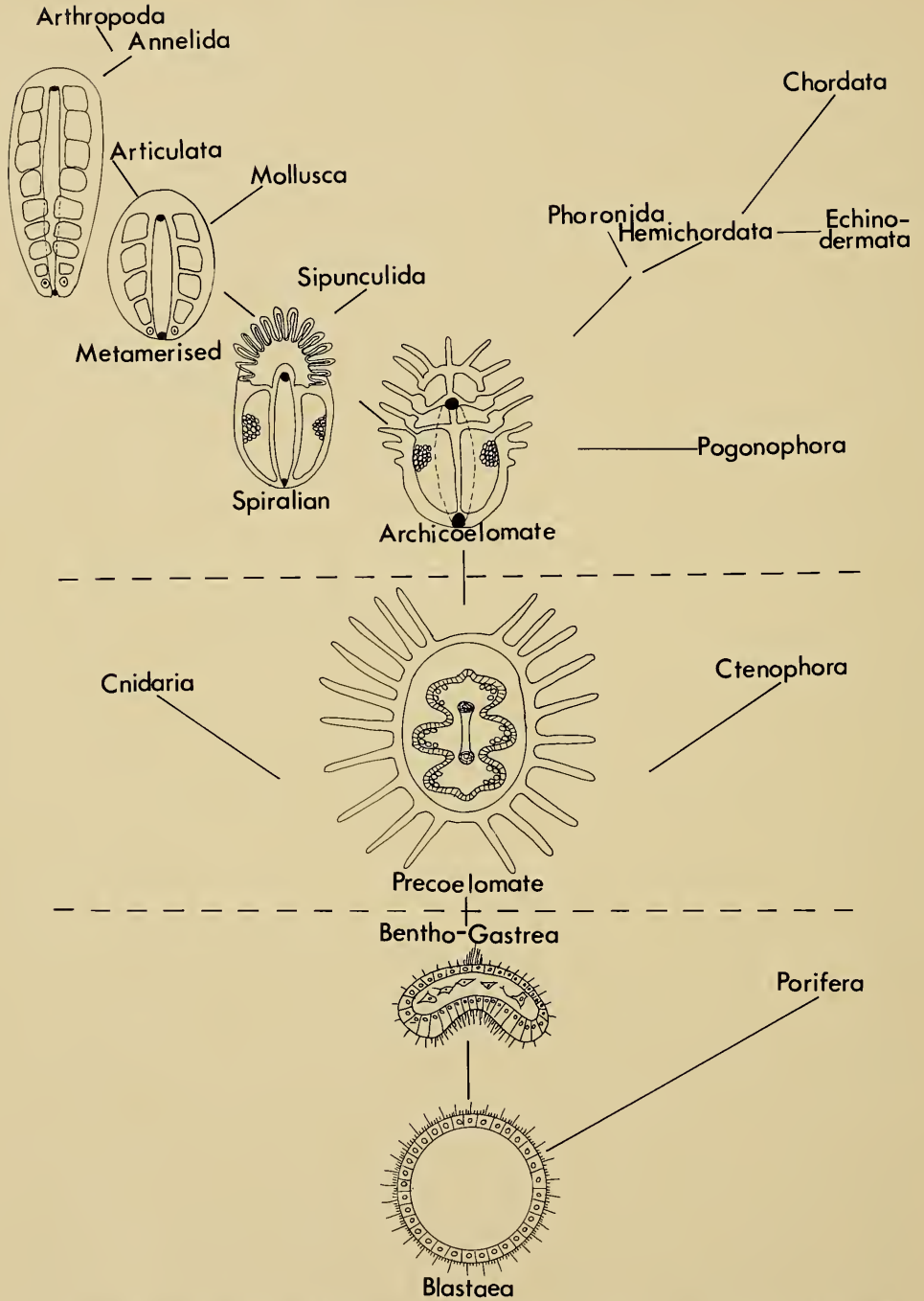


Fig. 3. The phylogenetic relationships of the Metazoa according to Siewing (1976), redrawn and simplified.

Nowadays, however, most zoologists and many palaeontologists have begun to include functional thinking in their phylogenetic interpretations (e.g. Bock, 1981; Szalay, 1981), though some palaeontologists still proceed in blissful unawareness of this need.

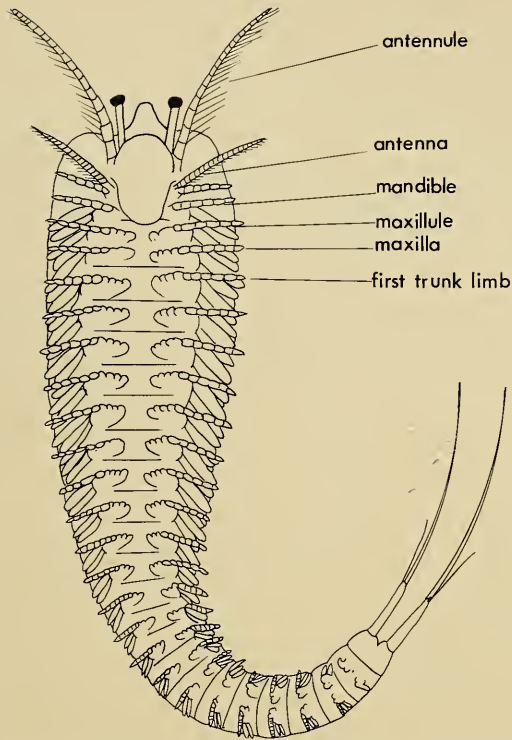


Fig. 4. The hypothetical urcrustacean of Hessler and Newman (redrawn after Hessler and Newman, 1973).

The speculations of Jefferies (Jefferies and Lewis, 1978; Jefferies, 1979, and earlier) on the Calcichordata as ancestral chordates exemplify this well, as Philip (1979) has remarked.

Curiously enough, this change of approach has led in turn to a third conceptual advance with a somewhat opposite effect. This is the realization that for the simpler kinds of animal organization, with few interacting components, it is very difficult to exclude the possibility of parallel or convergent evolution. Simple metazoans which may seem alike are not necessarily related. I shall return to this later.

#### FACTUAL ADVANCES

We are thinking about animal phylogeny with a new kind of honesty and understanding as a result of these conceptual changes, but this new approach derives basically from the availability of new facts about animals and their history. During the last twenty years, factual knowledge has advanced on three fronts pertinent to the problem of phylogenetic relationships. The early part of the fossil record of animals in the later Precambrian and Cambrian has become much better known (e.g. Brasier, 1979). The functional morphology of the modern phyla has become much better understood; and the embryonic development of many of the modern phyla has been more deeply analysed in functional terms. The interplay of fact and concept has now reached a stage at which the evidence of all three of these lines of investigation can be brought together in a more comprehensive way. I shall briefly review each area and then attempt to establish a synthesis from them.

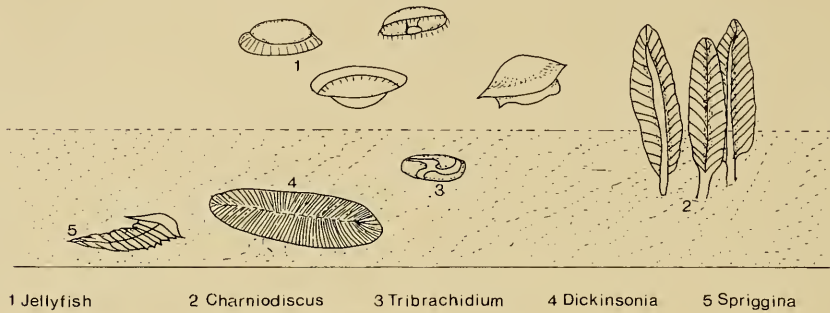


Fig. 5. Some representatives of the Ediacara fauna (after Glaessner).

### *The fossil evidence*

For the metazoan phyla, the fossil record of the later Precambrian is sparse but revealing (Durham, 1979; Paul, 1980; Runnegar, in press). It is well exemplified by the famous Ediacara fauna of South Australia and elsewhere, shown in Figure 5 (Glaessner, 1969, 1971, 1972, 1976, 1979, 1980; Glaessner and Wade, 1966; Wade, 1970, 1972; Ford, 1980; Birket-Smith, 1981). Beginning about 680 million years ago, cnidarians, polychaetes, echiuroids, arthropod-like animals and various other metazoans were already present. Evolution had thus reached the stage of complex, soft-bodied coelomate animals by the time metazoan fossils began to appear. This is further borne out by the appearance of pogonophorans before the onset of the Cambrian (Brasier, 1979) and a variety of complex skeletonized forms such as molluscs, echinoderms, brachiopods and trilobites (Figs 6, 7) in the early Cambrian (Runnegar, 1980a, and in press). This evidence tells us that the important separations of the metazoan phyla took place more than 700 million years ago, before any fossil metazoans were laid down. It also tells us that the fossils that are present all belong to discrete phyla, some modern, some extinct, and include no animals that can be interpreted as missing links. No new phyla are directly known to have evolved since the onset of the Cambrian, although some groups that might be accorded the status of phyla (Archaeocyatha, Hyolitha, Trilobita and others; see Fig. 25) became extinct in the Palaeozoic.

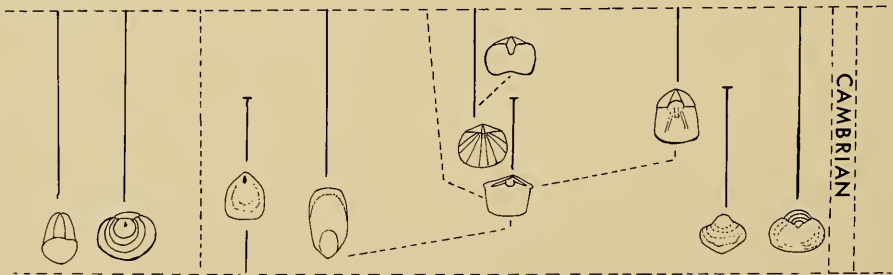


Fig. 6. The Cambrian evolution of the brachiopods (after Wright, 1979).

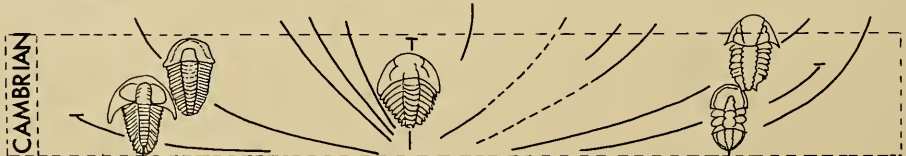
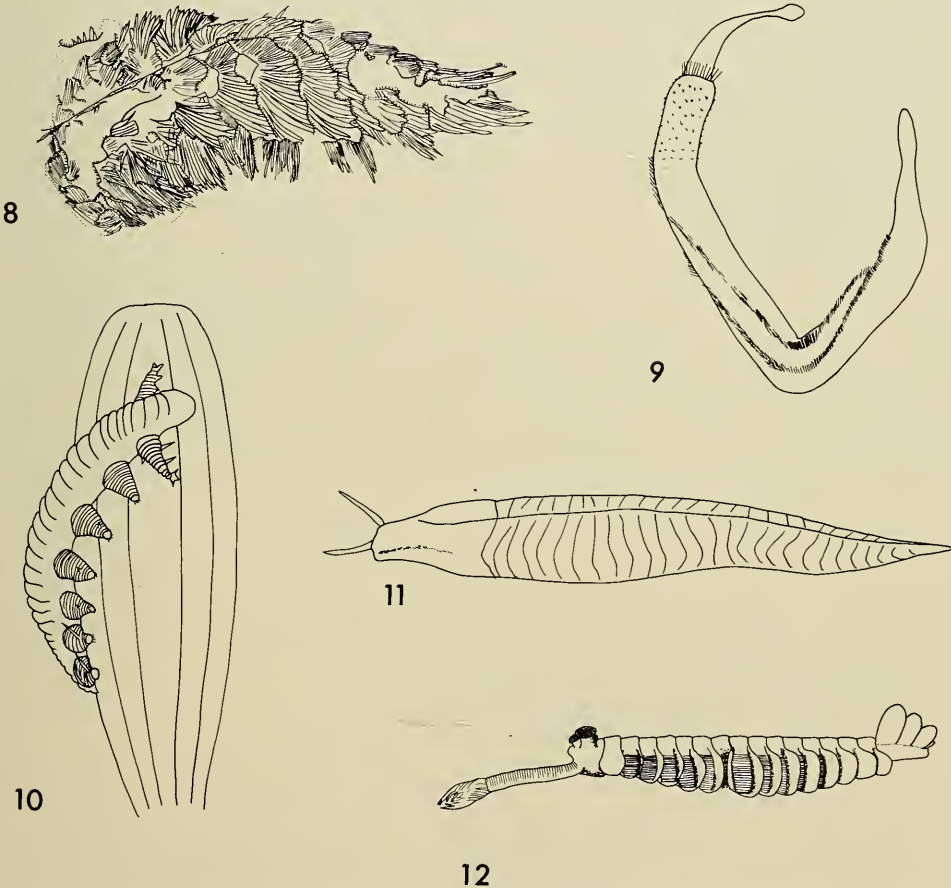


Fig. 7. The Cambrian evolution of the trilobites (after Bergström, 1979).

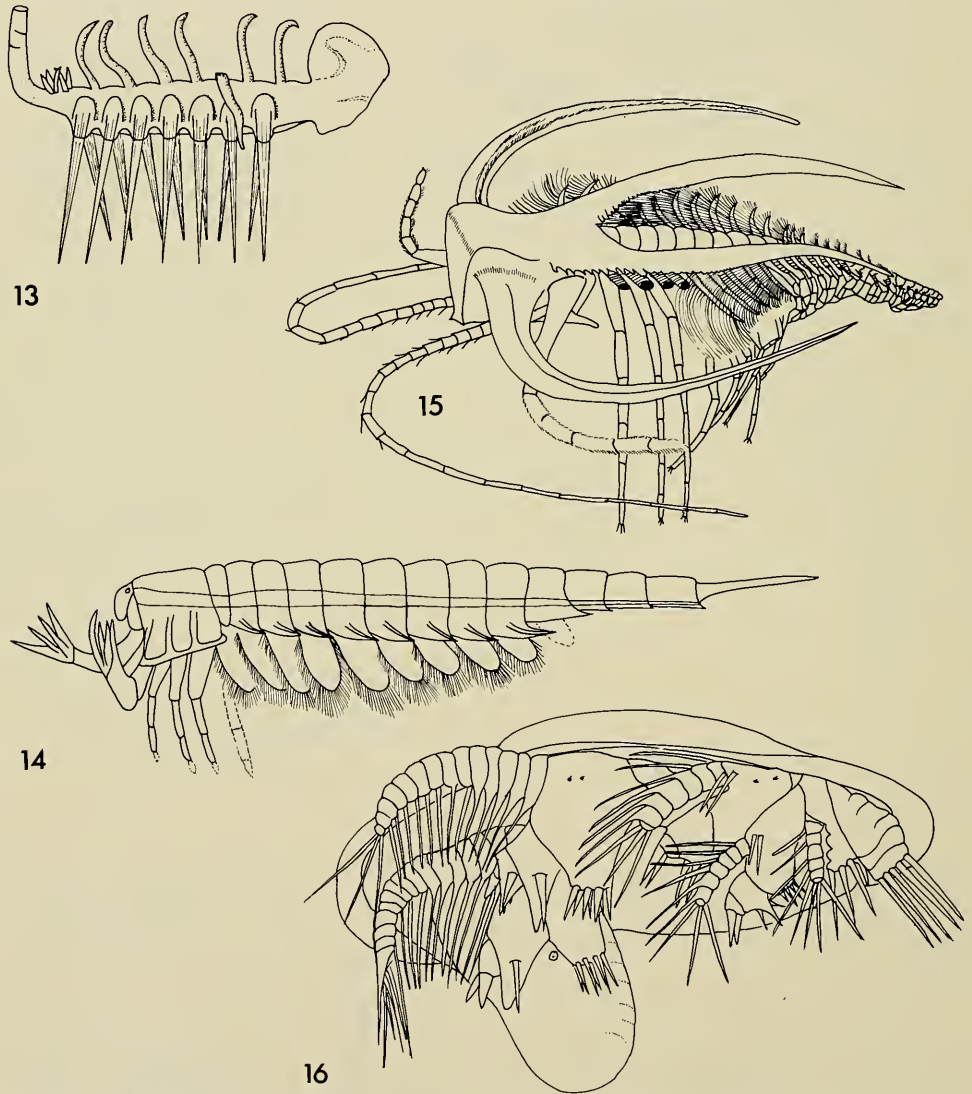
Confirmation of these conclusions arises from the recent studies of the Middle Cambrian Burgess Shale fauna (Conway Morris, 1979a; Whittington, 1979, 1980). In this work we find extraordinary evidence of the early presence of a variety of soft bodied animals belonging to modern phyla. The Burgess Shale fauna includes priapulids, polychaetes, marine uniramians and even chordates (Figs 8-11). The phylum Crustacea is also represented in the Burgess Shale by *Canadaspis*, and in the Upper Cambrian by ostracods (Fig. 16) and cephalocarids (Briggs, 1977; Müller, 1979, 1981).



Figs 8-12. 8, A polychaete of the middle Cambrian Burgess Shale (after Conway Morris, 1979b). 28 mm. 9, A priapulid of the middle Cambrian Burgess Shale (after Conway Morris, 1979a). 180 mm. 10, The middle Cambrian marine uniramian *Aysheaia* (redrawn from Whittington, 1980). 60 mm. 11, The middle Cambrian chordate *Pikaia* (based on Conway Morris and Whittington, 1979). 40 mm. 12, The middle Cambrian *Opabinia*, phylum unknown (after Whittington, 1980). 50 mm.

In addition, the Burgess Shale fauna contains many representatives of groups of animals that have not survived and do not belong within the modern phyla. These include such forms as *Opabinia* (Fig. 12), *Hallucigenia* (Fig. 13) and strange arthropods like *Yohoia* (Fig. 14), *Marrella* (Fig. 15) and *Odoraia* (Conway Morris, 1979a; Whittington, 1979, 1980, 1981a; Briggs, 1981). It seems that there were several (perhaps many) distinct groups of arthropods in the Cambrian fauna in

addition to the Trilobita, Crustacea, Chelicerata and Uniramia (Whittington, 1979, 1981b; Manton and Anderson, 1979). Whether *Opabinia*, *Hallucigenia*, the strange arthropods and the other unique animals of the Burgess Shale should be interpreted as members of discrete extinct phyla is debatable, but they are certainly indicative of the existence of Cambrian groups of animals that do not fit the definitions of any of the modern phyla. Like the Precambrian and early Cambrian metazoans, none of the Burgess Shale animals is intermediate between or directly ancestral to any of the recognized phyla. Their structural complexity, elucidated now in impressive detail, gives further evidence of a long prior history of metazoan evolution.



Figs 13-16. 13, The middle Cambrian *Hallucigenia*, a fossil worthy of a Bestiary (after Whittington, 1980). 18 mm. 14, The middle Cambrian arthropod *Yohoia*, phylum unknown (after Whittington, 1980). 23 mm. 15, The middle Cambrian arthropod *Marrella*, phylum unknown (after Whittington, 1980). 20 mm. 16, The upper Cambrian ostracod *Vestrogothia* (after Müller, 1979). 0.5 mm.



From the point of view of the origins and relationships of the animal phyla, then, the fossil evidence provides nothing directly, except a confirmation of the timing of events. This puts the onus directly on functional morphology and embryology to provide some answers within this context.

### *Functional morphology*

Curiously enough, what this discipline has done for phylogenetic relationships among the animal phyla is mostly negative. The recognition that animals are highly functionally integrated and adapted in relation to habit and habitat has led to the further realization that they are often more different than they seem. Common ancestries then become much less plausible. The separation of the arthropods into three modern phyla and probably several extinct phyla (Anderson, 1973; Manton, 1973, 1977; Schram, 1978; Manton and Anderson, 1979; Whittington, 1979, 1981b) is perhaps the most spectacular example of how functional morphology has demolished old beliefs, but there are others. The fact that structure is functionally related to habit and habitat is well illustrated in a broad sense by the case of the coelomic worms. Functional studies (Clark, 1979) have demonstrated a clear relationship between:

1. an unsegmented coelom and burrowing slowly in compact substrata,
2. a segmented coelom and burrowing actively in looser substrata,
3. a trimeric coelom and tubicolous life.

Each of these conditions could have evolved independently more than once and none needs any other as a functional prerequisite. For example, there is no reason to suppose on functional morphological ground that the Sipunculida and the Priapulida, both unsegmented coelomate burrowers, are related to one another. The Phoronida and the Pogonophora both show a trimeric tubicolous condition, but the

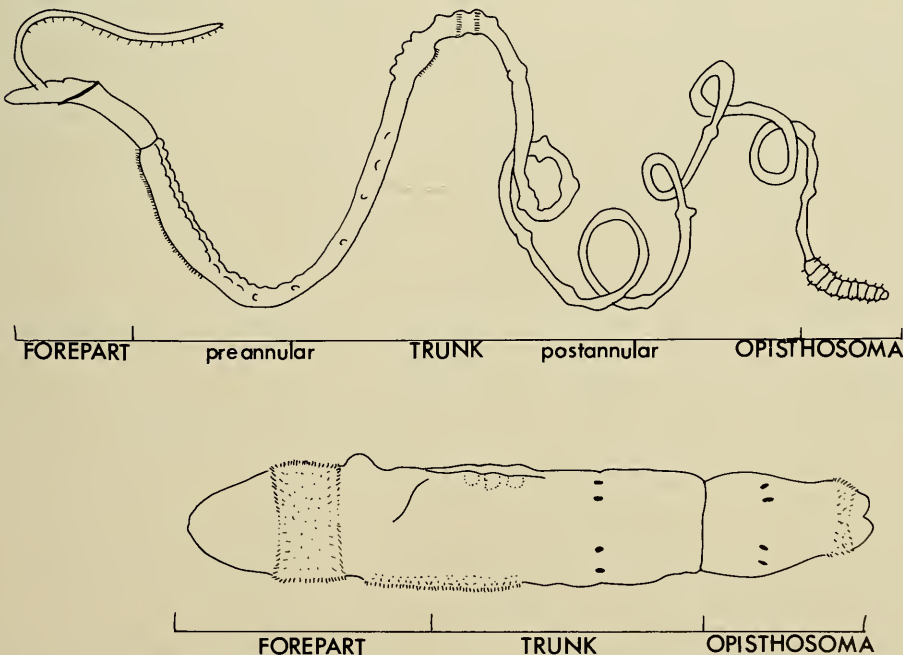


Fig. 17. The adult and larva of a pogonophoran (after Southward, 1980).

Pogonophora (Fig. 17) are now thought to be specialized descendants of the annelids (Southward, 1980; Jones, 1981), while phoronids are clearly lophophorates (Zimmer, 1973; Hermann, 1980). The trimeric coelomate condition, therefore, has evolved more than once and of itself is not evidence for phylogenetic affinity, only of adaptation to tubicolous life. Even tubicolous polychaetes such as serpulids tend to a trisomic condition, while retaining metameric segmentation.

This case epitomizes the general effect of functional morphology on phylogenetic thinking. It has made us more wary of overemphasizing general resemblances and more honest about the gaps in the story. It has also made us realize the likelihood of convergent evolution among complex phyla and even more, the likelihood of convergent evolution among the animals of the simpler phyla. On the other hand, functional morphology has not assisted in the positive identification of interphylum relationships, except perhaps in relating ectoprocts to endoprocts (Nielsen, 1977) and pogonophorans to annelids (Southward, 1980).

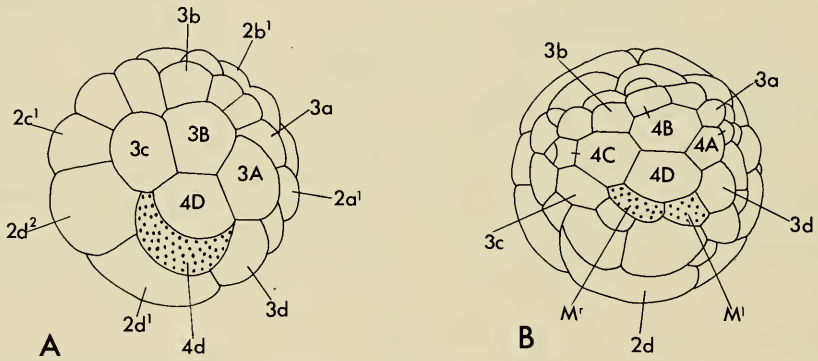


Fig. 18. Typical stages in polychaete spiral cleavage, (a) *Arenicola* (b) *Amphitrite* (after Anderson, 1973).

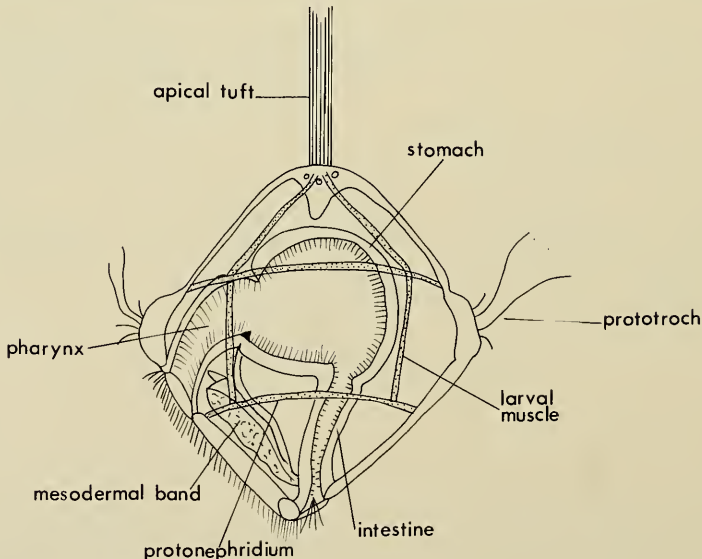


Fig. 19. A polychaete trochophore larva.

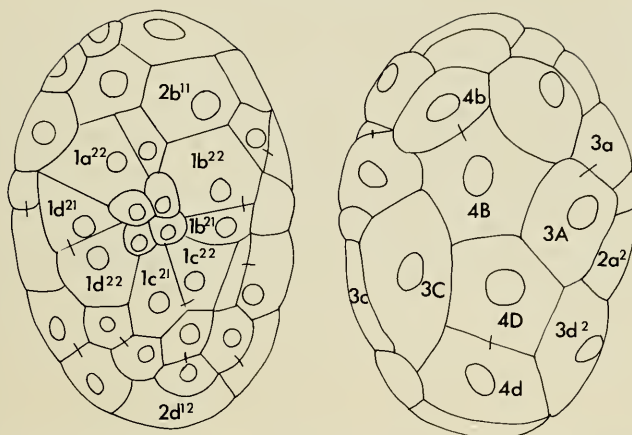


Fig. 20. Stages in the spiral cleavage of the egg of the pogonophoran *Nereilinum murmanicum* (after Gureeva, 1979).

### Comparative embryology

Where, then, are we to turn for evidence of phylogenetic relationships between phyla? Fortunately, for a number of phyla, an answer still lies in embryology. Detailed functional analyses of development have shown that developmental patterns can remain astonishingly conservative despite wide divergences in adult form and complexity. It is necessary, of course, to make allowance for functional specializations of the developmental process in relation to its own requirements such as planktotrophic adaptations and/or the presence of yolk in the embryo. Taking these into account, we can discern certain well-established cases where embryological studies strongly indicate phylogenetic affinities. Spiral cleavage development is one such case.

The pattern of spiral cleavage development which includes 4d mesoderm and a subsequent larva of the trochophore type (Figs 18-20) links many phyla, including molluscs, annelids, pogonophorans and uniramians, with the platyhelminths (Anderson, 1973, 1979; Gureeva, 1979; Bakke, 1980). Mostly these phyla cannot be positively linked on other evidence. Other kinds of spiral cleavage development occur in other phyla, linking them more remotely to the 4d group. These include (Figs 21, 22) rotifers, gastrotrichs, nematodes and crustaceans (Anderson, 1973, 1979, in press; Joffe, 1979). Another major grouping on embryological grounds is recognizable from the radial cleavage, deuterostome, trimeric pattern of development which links the hemichordates, chordates, echinoderms and chaetognaths (Philip, 1979; Hermann, 1980, Pross, 1980). This kind of evidence works well for complex animals where enough information is available, though a number of groups of complex animals have still not been investigated sufficiently to allow phylogenetic inferences to be drawn about them in embryological terms.

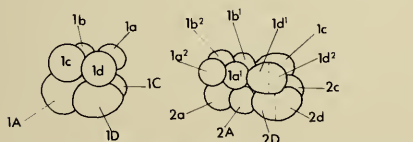


Fig. 21. Stages in the spiral cleavage of the egg of a rotifer, *Neogosseia* (after Joffe, 1979).

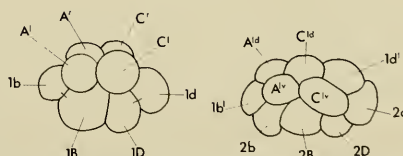


Fig. 22. Stages in the cleavage of the egg of a nematode, *Prionchulus* (after Joffe, 1979).

Embryological evidence is not satisfactory, on the other hand, for the simpler groups, where development offers less information. Sponges, ctenophores and cnidarians cannot be related to each other or to other phyla on embryological grounds. The need for an integrated functional interpretation of the sequence of development must also be emphasized. Evidence of this kind, when incomplete, is easily misused. Attempts to relate the Pycnogonida to the Chelicerata and the Pentastomida to the branchiuran Crustacea (Riley *et al.*, 1978; Schram, 1978) on the basis of inadequate description of a few embryo stages (Fig. 23) must remain totally unconvincing, though there are good functional morphological reasons why the pycnogonids should be included in the phylum Chelicerata (Manton, 1978; Bergstrom *et al.*, 1980).

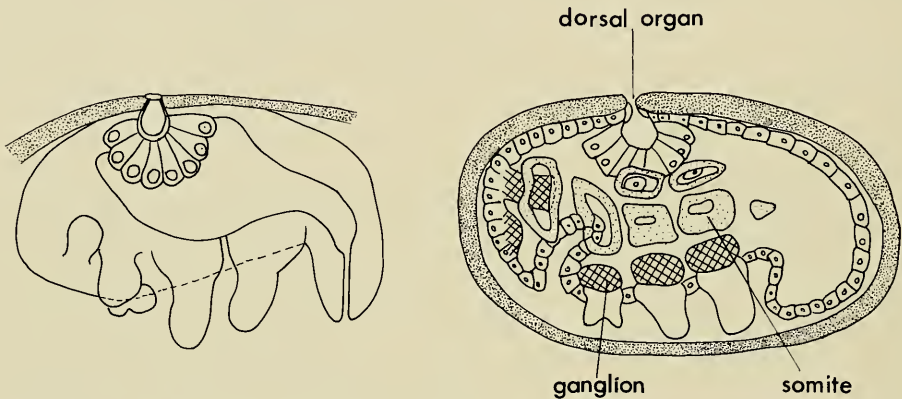


Fig. 23. Two stages in the embryonic development of the pentastomid *Reighardia sternae* (after Riley *et al.*, 1978).

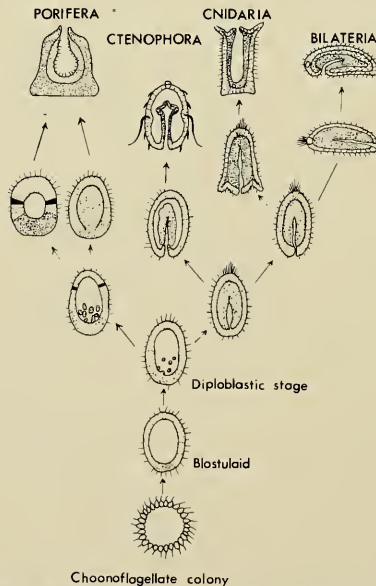


Fig. 24. The phylogeny of the Radialia, as interpreted by Salvini-Plawen (1978)

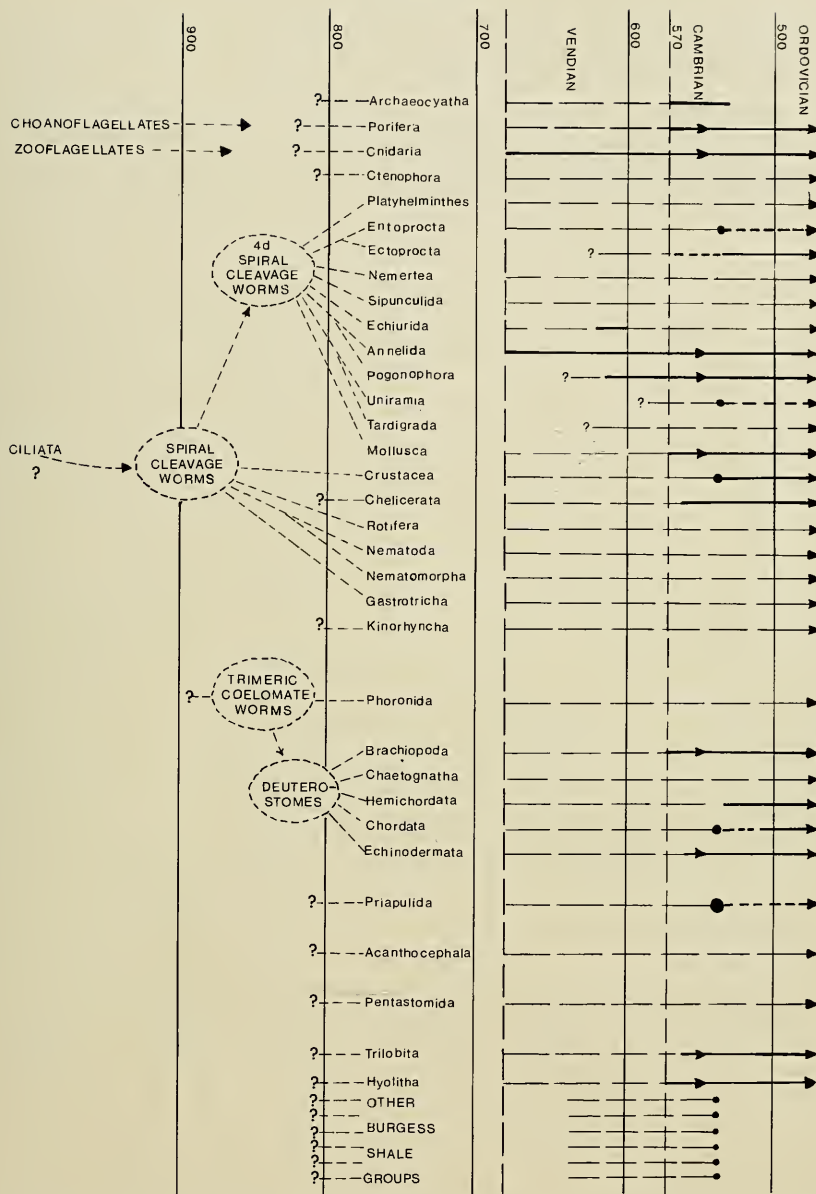


Fig. 25. A summation of the fossil, functional morphological and embryological evidence for the origins and relationships of the animal phyla. Known fossil histories since the beginning of the Vendian are indicated by solid lines. Evolutionary histories deduced from comparative evidence (see text) are shown by broken lines. The solid circles at the level of the Middle Cambrian represent the Burgess Shale fauna.

All of the known animal phyla had a Precambrian origin. Most (probably all) had a pre-Vendian origin. All modern phyla may thus have been in existence for at least 700 million years. The Archaeocyatha became extinct during the Cambrian (Nitecki and Debrenne, 1979). The Trilobita and Hyolitha became extinct at the end of the Palaeozoic (Bergström, 1979; Runnegar, 1980b). The time of extinction of the 'Burgess Shale groups' is unknown, but there is no record of them after the middle Cambrian.

Embryological evidence reveals the pattern of divergence of the animal phyla shown on the left of the Figure. These events must have occurred between 1,000 and 700 million years ago. Several major ancestral groups can be recognized. A number of significant questions remain to be resolved.

Embryological evidence can also be misused in other ways, as when simple embryos are taken as direct evidence of affinity (Salvini-Plawen, 1978), and then in a double dose of conceptual legerdemain, also interpreted in a recapitulationist manner as representative of adult ancestors (Fig. 24). If embryology is to be useful in establishing phylogenetic relationships, which it can be in many cases, we must guard carefully against such simplistic thinking. This is especially important when we now realize that herein lies the major source of our positive information on the matter.

#### AN ATTEMPT AT INTEGRATION

Supposing that we now take these various lines of evidence and put them together, where do we stand? An attempt at an integrated generalization is made in Fig. 25. The direct fossil evidence leads us to a reasonable presumption of a prior history of the phyla through time, but neither the fossil evidence nor that of functional morphology provides much indication of common ancestries. Two major groupings of phyla, with initial radiations at the soft-bodied worm-like stage, can be identified embryologically. These radiations, the spiral cleavage radiation and the deuterostome radiation, probably occurred more than 700 million years ago. Runnegar (in press) has estimated, from comparative data on the molecular structure of invertebrate globins, that the initial radiations of metazoan animals began about 1,000 million years ago, so that at least 300 million years appears to have been available for the early evolution and diversification of these two major groups. At the present time, the original history of the remaining phyla cannot be traced, though further embryological analysis and further discoveries in the fossil record may assist with this.

Another point is now extremely evident, amplifying an idea developed on theoretical grounds in a thoughtful essay by Kerkut (1960). There is no compelling reason to suppose that the metazoan phyla had a single origin. The trimeric coelomates, which cannot presently be traced to a simpler ancestry, share no features in common with the spiral cleavage phyla. More than one origin of metazoans from protozoans remains a real possibility. The sponges, cnidarians and ctenophores are fundamentally different from each other and from the bilateral phyla. They could, as Sleigh (1979) has suggested, have had separate origins. Future workers on this problem should also bear in mind that two or more kinds of bilateral phyla may have emerged independently from among the Protozoa, though plainly the embryological evidence shows that we cannot go as far in this as the proposal by Nursall (1962), of a separate origin of each metazoan phylum from a protozoan ancestry. Future detailed studies in comparative embryology and palaeontology may indeed reveal the exact opposite, that the metazoan phyla of presently unknown ancestry are linked with one or the other of the clearly identifiable major assemblages.

#### ACKNOWLEDGEMENTS

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#### References

- ANDERSON, D. T., 1967. — Morphological integration and animal evolution. *Scientia* 102: 1-6.  
 ———, 1973. — *Embryology and Phylogeny in Annelids and Arthropods*. Oxford: Pergamon.  
 ———, 1979. — Embryos, fate maps and the phylogeny of arthropods. pp. 59-105 in GUPTA, A. P., (ed.), *Arthropod phylogeny*. New York: Van Nostrand Reinhold.

- , (in press) — Embryology of Crustacea. In ABELE, L., (ed.), *The Biology of Crustacea*. Volume 2. New York: Academic Press.
- BAKKE, T., 1980. — Embryonic and postembryonic development in the Pogonophora. *Zool. Jb. Anat.* 103: 276-284.
- BARNES, R. D., 1968. — *Invertebrate zoology*. Philadelphia: W. B. Saunders.
- BERGSTRÖM, J., — 1979. — Morphology of fossil arthropods as a guide to phylogenetic relationships. pp. 3-56 in GUPTA, A. P., (ed.), *Arthropod Phylogeny*. New York: Van Nostrand Reinhold.
- , STÜRMER, W., and WINTER, B., 1980. — *Palaeoisopus*, *Palaeopantopus* and *Palaeothea*, pycnogonid arthropods from the lower Devonian Hunsrück Slate, West Germany. *Palaeont. Z.* 54: 5-54.
- BIRKET-SMITH, S. J. R., 1981. — A reconstruction of the Precambrian *Spriggina*. *Zool. Jb. Anat.* 105: 237-258.
- BOCK, W. J., 1981. — Functional adaptive analysis in evolutionary classification. *Amer. Zool.* 21: 5-20.
- BRASIER, M. D., 1979. — The Cambrian radiation event. pp. 103-159 in HOUSE, M. R., (ed.), *The origins of major invertebrate groups*. London: Academic Press.
- BRIGGS, D. E. G., 1977. — The morphology, mode of life and affinities of *Canadaspis perfecta* (Crustacea Phyllocarida), middle Cambrian, Burgess Shale, British Columbia. *Phil. Trans. Roy. Soc. B* 281: 439-487.
- , 1981. — The arthropod *Odaraiia alata* Walcott, Middle Cambrian, Burgess Shale, British Columbia. *Phil. Trans. Roy. Soc. B* 291: 541-585.
- CLARK, R. B., 1979. — Radiation of the Metazoa. pp. 55-102 in HOUSE, M. R., (ed.), *The origins of major invertebrate groups*. London: Academic Press.
- CONWAY MORRIS, S., 1979a. — The Burgess Shale (Middle Cambrian) fauna. *Ann. Rev. Ecol. Syst.* 10: 327-349.
- , 1979b. — Middle Cambrian polychaetes from the Burgess Shale of British Columbia. *Phil. Trans. Roy. Soc. B* 285: 227-274.
- , and WHITTINGTON, H. B., 1979. — The animals of the Burgess Shale. *Scientific American* 241 (1): 110-121.
- DULLEMEIJER, P., 1980. — Functional morphology and evolutionary biology. *Acta Biotheoretica* 29: 151-250.
- DURHAM, J. S., 1978. — The probable metazoan biota of the Precambrian as indicated by the subsequent record. *Ann. Rev. Earth Planet. Sci.* 6: 21-42.
- FORD, T. D., 1980. — The Ediacaran fossils of Charnwood Forest, Leicestershire. *Proc. Geol. Ass.* 91: 81-83.
- GLAESSNER, M. F., 1969. — Trace fossils from the Precambrian and basal Cambrian. *Lethaia* 2: 369-393.
- , 1971. — Geographic distribution and time range of the Ediacara Precambrian fauna. *Geol. Soc. Amer. Bull.* 82: 509-514.
- , 1972. — Precambrian palaeozoology. *Univ. Adelaide Centre for Precambrian Res., Spec. Pap.* 1: 43-52.
- , 1976. — Early Phanerozoic annelid worms and their geological and biological significance. *J. Geol. Soc. (Lond.)* 132: 259-275.
- , 1979. — An echiurid worm from the Late Precambrian. *Lethaia* 12: 121-124.
- , 1980. — *Parvancorina* — an arthropod from the Late Precambrian (Ediacarian) of South Australia. *Ann. Naturhist. Mus. Wien* 83: 83-90.
- , and WADE, M., 1966. — The Late Precambrian fossils from Ediacara, South Australia. *Palaeontology* 9: 599-628.
- GUREEVA, M. A., 1979. — A contribution to the study of the early development of *Nereilinum murmanicum* Ivanov, 1961 (Pogonophora). *Proc. Zool. Inst., Acad. Sci. USSR*, 84 Leningrad: 63-72.
- GUTMANN, W. F., 1981. — Relationships between invertebrate phyla based on functional mechanical analysis of the hydrostatic skeleton. *Amer. Zool.* 63-81.
- HERRMANN, K., 1980. — Die archimere Gliederung bei *Phoronis mülleri* (Tentaculata). *Zool. Jb. Anat.* 103: 234-249.
- HESSLER, R. R., and NEWMAN, W. A., 1973. — A trilobitormorph origin for the Crustacea. *Fossils and Strata* 4: 437-459.
- JEFFERIES, R. P. S., 1979. — The origin of chordates — a methodological essay. pp. 443-477 in HOUSE, M. R., (ed.), *The origins of major invertebrate groups*. London: Academic Press.
- , and LEWIS, D. N., 1978. — The English Silurian fossil *Placocystites forbesianus* and the ancestry of the vertebrates. *Phil. Trans. Roy. Soc. B* 282: 205-323.
- JOFFE, B. I., 1979. — The comparative embryological analysis of the development of Nematelminthes. *Proc. Zool. Inst. Acad. Sci. USSR*, 84 Leningrad: 39-62.
- JONES, M. L., 1981. — *Riftia pachyptila* Jones: observations on the vestimentiferan worm from the Galapagos Rift. *Science* 209: 333-336.

- KERKUT, G. A., 1960. — *Implications of evolution*. Oxford: Pergamon.
- MANTON, S. M., 1973. — Arthropod phylogeny — a modern synthesis. *J. Zool., Lond.* 171: 111-130.
- , 1977. — *The Arthropoda: Habits, functional morphology and evolution*. Oxford: Oxford University Press.
- , 1978. — Habits, functional morphology and evolution of pycnogonids. *Zool. J. Linn. Soc.* 63: 1-22.
- , and ANDERSON, D. T., 1979. — Polyphyly and the evolution of arthropods. pp. 269-321 in HOUSE, M. R., (ed.), *The origins of major invertebrate groups*. London: Academic Press.
- MÜLLER, K. J., 1979. — Phosphatocopine ostracods with preserved appendages from the Upper Cambrian of Sweden. *Lethaia* 12: 1-27.
- , 1981. — Arthropods with phosphatized soft parts from the Upper Cambrian 'Orsten' of Sweden. *U.S. Geol. Survey, Open File Rep.* 81-743: 147-151.
- NIELSEN, C., 1977. — The relationship of Endoprocta, Ectoprocta and Phoronida. *Amer. Zool.* 17: 149-152.
- NITECKI, M. H., and DEBRENNE, F., 1979. — The nature of radiocyathids and their relationship to receptaculitids and archaeocyathids. *Géobios* 12: 5-27.
- NURSALL, J. R., 1962. — On the origins of the major groups of animals. *Evolution* 16: 118-123.
- PAUL, C., 1980. — *The natural history of fossils*. London: Weidenfeld and Nicholson.
- PHILIP, G. M., 1979. — Carpoids — echinoderms or chordates? *Biol. Rev.* 54: 439-471.
- PROSS, A., 1980. — Untersuchungen zur Gliederung von *Lingula anatina* (Brachiopoda). Archimerie bei Brachiopoden. *Zool. Jb. Anat.* 103: 250-263.
- RILEY, J., BANAJA, A. A., and JAMES, J. L., 1978. — The phylogenetic relationships of the Pentastomida: The case for their inclusion within the Crustacea. *Int. J. Parasitol.* 8: 245-254.
- RUNNEGAR, B., 1980a — Mollusca: The first hundred million years. *J. malacol. Soc. Aust.* 4: 223-224.
- , 1980b. — Hyolitha: Status of the phylum. *Lethaia* 13: 21-25.
- , (in press) — The Cambrian explosion: Animals or fossils. *J. Geol. Soc. Aust.*
- SALVINI-PLAWEN, L. V., 1978. — On the origin and evolution of the lower Metazoa. *Z. zool. Syst. Evolut.forsch.* 16: 40-88.
- SCHRAM, F. R., 1978. — Arthropods: A convergent phenomenon. *Fieldiana, Geol.* 39: 61-108.
- SIEWING, R., 1976. — Probleme und neuere Erkenntnisse in der Gross-systematik der Wirbellosen. *Verh. Dtsch. zool. Ges.* 1976: 59-83.
- SLEIGH, M. A., 1979. — Radiation of the eukaryote Protista. pp. 23-53 in HOUSE, M. R., (ed.), *The origins of major invertebrate groups*, London: Academic Press.
- SOUTHWARD, E. C., 1980. — Regionation and metamerisation in Pogonophora. *Zool. Jb. Anat.* 103: 264-275.
- SZALAY, F. S., 1970. — Functional analysis and the practice of the phylogenetic method as reflected by some mammalian studies. *Amer. Zool.* 21: 37-45.
- WADE, M., 1970. — The stratigraphic distribution of the Ediacara fauna in Australia. *Trans. Roy. Soc. S. Aust.* 94: 87-104.
- , 1972. — *Dickinsonia*: Polychaete worms from the late Precambrian Ediacara fauna, South Australia. *Mem. Qld. Mus.* 16: 171-190.
- WHITTINGTON, H. B., 1979. — Early arthropods, their appendages and relationships. pp. 253-268 in HOUSE, M. R., (ed.), *The origins of major invertebrate groups*. London: Academic Press.
- , 1980. — The significance of the fauna of the Burgess Shale, Middle Cambrian, British Columbia. *Proc. Geol. Ass.* 91: 127-148.
- , 1981a. — Rare arthropods from the Burgess Shale, Middle Cambrian, British Columbia. *Phil. Trans. Roy. Soc. B* 292: 329-357.
- , 1981b. — Cambrian animals: Their ancestors and descendants. *Proc. Linn. Soc. N.S.W.*, 105: 79-87.
- WRIGHT, A. D., 1979. — Brachiopod radiation. pp. 235-252 in HOUSE, M. R., (ed.), *The origins of major invertebrate groups*. London: Academic Press.
- YONGE, C. M., and THOMPSON, T. E., 1976. — *Living marine molluscs*. London: Collins.
- ZIMMER, R. L., 1973. — Morphological and developmental affinities of the lophophorates. pp. 593-599 in LARWOOD, G. P., (ed.), *Living and fossil Bryozoa, Recent advances in research*. London: Academic Press.